New *Sthenurus* Species (Macropodidae, Diprotodontia) from Wellington Caves and Bingara, New South Wales

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Two new species of the extinct macropodid genus *Sthenurus* are described from vertebrate deposits in eastern and northeastern New South Wales. Although its exact stratigraphic origin is uncertain, *Sthenurus brachyselenis* sp. nov. displays an early stage of evolution, only slightly more derived than the plesiomorphic early Pliocene *S. cegsai*. Its molars are low crowned and relatively simple, and P^3 bears a very short buccal crest. *S. euryskaphus* sp. nov. is from the Pleistocene Bingara deposit and is morphologically intermediate between the late Pliocene *S. antiquus* and two widespread Pleistocene species. *S. oreas*, within which the two new species were previously included, is deemed to be a very derived member of the genus, and may reside phylogenetically close to the origin of *Procoptodon*.

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KEYWORDS: Sthenurine kangaroo, *Sthenurus, Simosthenurus, Sthenurus brachyselenis* sp. nov., *Sthenurus euryskaphus* sp. nov., *Sthenurus oreas*, Wellington Caves, Bingara, Pliocene, Pleistocene.

INTRODUCTION

Sthenurine kangaroos (subfamily Sthenurinae) are considered to have diverged from macropodine kangaroos (subfamily Macropodinae) in the mid-late Miocene (Flannery 1989). Although rare in Pliocene deposits, they are diverse and abundant in Pleistocene faunas, and distributed across much of southern and eastern Australia (Tedford 1966). This paper describes a new species of *Sthenurus,* probably of Pliocene age from Wellington Caves, eastern New South Wales, and another species from a Pleistocene deposit near Bingara in northern New South Wales.

Following Tedford's (1966) subgeneric division of *Sthenurus,* both new species described here would be referred to *Simosthenurus,* based on their relatively low crowned molars, upturned lower incisors and shortened mandibles. However, current research by one of us (GJP) questions the validity of the subgeneric or generic (*sensu* Flannery 1983) distinction within *Sthenurus.*

MATERIALS AND METHODS

Material referable to the new species is housed in the Australian Museum (prefix AM). Dental homology employed is that of Flower (1867) following Luckett (1993) and Ride (1993). Dental nomenclature follows Tedford and Woodburne (1987) and Ride (1993). Mensuration follows Tedford (1966) and Wells and Murray (1979), with all measurements in millimetres and listed in Table 1: Anterior Width = width of protolophid; Posterior Width = width of hypolophid; Anterior Height = height of protolophid crown on buccal side; Posterior Height = height of hypolophid crown on buccal side. Comparisons have generally been made with those taxa that appear most similar to the two new species.

Specimens and localities used for comparisons are listed in the Appendix.

TABLE 1

Cheek teeth dimensions of *Sthenurus brachyselenis* and *S. euryskaphus*. Values in millimetres.

Tooth	Species	Length	Anterior Width	Posterior Width	Anterior Height	Posterior Height
P_2	*S. brachyselenis*	8.1	5.1	6.1	5.7	5.5
dP_3	*S. brachyselenis*	10.2	7.8	8.2	6.2	7.0
	S. euryskaphus	9.4	7.8	7.9	6.5	6.5
P_3	*S. brachyselenis*	13.8	6.3	8.0	7.3	6.7
	S. euryskaphus	13.9	7.0	8.7	9.5	8.7
M_1	*S. brachyselenis*	13.9	9.9	10.3	9.3	9.4
	S. euryskaphus	12.9	9.7	9.7	8.4	8.4
M_2	*S. brachyselenis*	–	–	–	–	–
	S. euryskaphus	*14.4*	*10.8*	*10.9*	*9.0*	*8.5*

SYSTEMATICS

Order DIPROTODONTIA Owen 1866
Suborder PHALANGERIDA Aplin and Archer 1987
Superfamily MACROPODOIDEA (Gray 1821)
Family MACROPODIDAE Gray 1821
Subfamily STHENURINAE (Glauert 1926)
Genus *STHENURUS* Owen 1874
Subgenus *SIMOSTHENURUS* Tedford 1966

Sthenurus (Simosthenurus) brachyselenis sp. nov.
(Figs 1–3)
1966 *Sthenurus oreas* Tedford, p. 39–40.

Holotype

AM F31026, right juvenile ramus with I_1, P_2, dP_3, M_1 erupted; M_2 in early stage of eruption; and P_3 excavated from body of mandible. Only ventral portion of ascending ramus is preserved.

Type locality and age

The holotype is from Wellington Caves, eastern New South Wales (32°31'S, 148°51'E) and was collected in 1932 by C. Anderson and W. Schevill from a phosphate

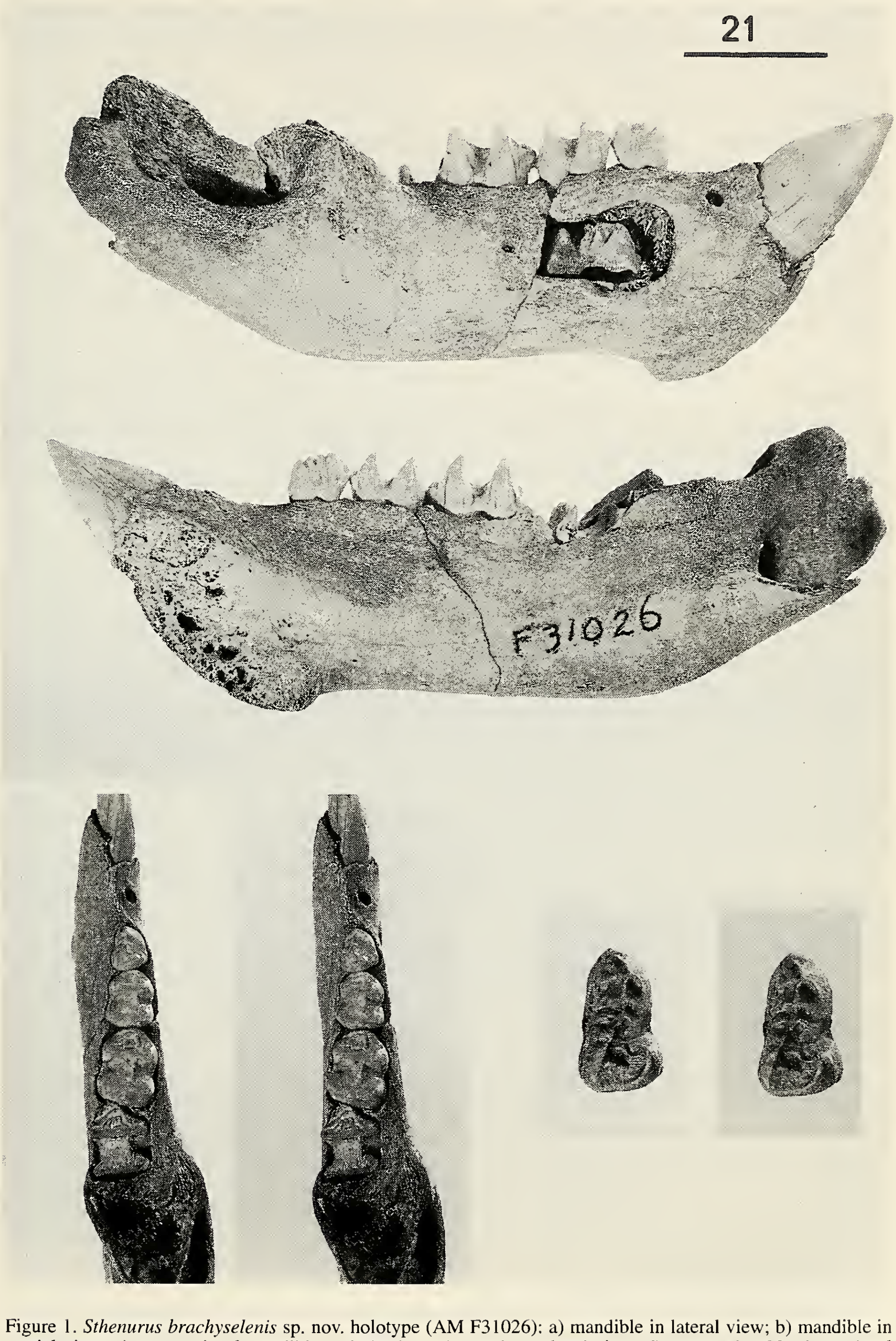

Figure 1. *Sthenurus brachyselenis* sp. nov. holotype (AM F31026): a) mandible in lateral view; b) mandible in mesial view; c) stereopair of mandible and cheek tooth row in occlusal view; d) stereopair of P_3 in occlusal view. Scale in millimetres.

mining drive (Anderson 1932, Dawson 1985). The stratigraphic provenance of the specimen is unknown, although the species appears to exhibit a Pliocene stage of evolution.

Diagnosis

I_1 robust with relatively straight occlusal surface, only very slightly curved dorsally at anterior extreme. P_2 short relative to length of dP_3, possessing very short, crescentic buccal crest. This crest extends from posterior extremity of main (lingual) crest, terminates in posterobuccal corner and extends only very slightly anteriorly. P_3 short, equal in length to M_1, narrow and only inflated in posterobuccal corner below very short, crescentic buccal crest. This crest extends only one-third length of tooth. Anterior cingulum of lower molars symmetrically tapered, from both buccal and lingual extremities of protolophid.

Etymology

Gr. *brachys* 'short', *selenis* 'crescent', in reference to the short crescentic nature of the buccal crest on P_2 and P_3.

Description

Juvenile mandible with ramus relatively deep and narrow for much of its length. Prominent boss extends below level of ventral border of ramus at base of symphysis. Symphysis extends posteriorly below circular genial pit. Digastric sulcus very shallow and digastric eminence only moderately formed. Diastema very short and orientated in same plane as I_1 occlusal surface. Buccinator sulcus narrow, deep and positioned close to dorsal border of ramus, extending from between anterior mental foramen and half-way point on diastema, to below hypolophid of dP_3. Dorsal border of anterior mental foramen located immediately below anterior extreme of buccinator sulcus. Posterior mental foramen positioned directly below protolophid of M_1, on a horizontal plane that lies just below ventral border of masseteric fossa. Masseteric foramen elongate when viewed dorsally, leading into slightly anteroventrally trending masseteric canal. Inferior mandibular foramen moderately sized and ovally-shaped.

I_1 robust and upturned relative to cheek tooth row, with occlusal surface long and straight, and orientated in same plane as diastema. Anterior extreme of occlusal surface only very slightly curved dorsally.

P_2 short relative to length of dP_3, with main (lingual) crest consisting of four prominent cuspules, posteriormost largest. Transverse ridge directed buccally from posterior extreme of main crest and confluent with a very short crescentic buccal crest. Posteriorly directed ridgelet descends from second cuspule on main crest, terminating immediately anterior to buccal crest and resulting in a small notch.

dP_3 completely molariform, with protolophid tapering more toward narrower occlusal surface than hypolophid. Cristid obliqua and paracristid fine and low. Lophid faces lack enamel crenulations. Paracristid relatively short, descending anterolingually from protoconid apex, then trending more anteriorly and bifurcating. Main component of this curves lingually, while minor short ridge extends anteriorly to edge of anterior cingulum. A weak premetacristid folds across anterior face of protolophid into trigonid basin, terminating before reaching anterolingually directed component of paracristid. Posterior face of hypolophid bears a weak, centrally positioned, triangular-shaped inflation, with point of triangle uppermost.

Unerupted P_3 short and equal in length to M_1, although not yet bearing full complement of enamel. P_3 narrow and dominated by main (lingual) crest, except for expanded posterobuccal corner upon which short, crescentic buccal crest is borne. Buccal crest extends one-third length of tooth. Main crest divided into five cuspules, with posteriormost twice size of any of anterior four. Three anteriormost cuspules accompanied by finer lingual and coarser buccal vertical ridgelets. Two transverse ridgelets cross median valley between main and buccal crests, arising from buccal face of posteriormost cuspule on main crest, then extending to base of lingual face of buccal crest. A transverse ridge connects posteroventral extreme of main crest to buccal crest with which ridge is confluent.

M_{1-2} low crowned with protolophid and hypolophid occlusal surfaces linear and close to parallel. Cristid obliqua and paracristid low, but well-formed, and remaining close to buccal side of tooth. Anterior cingulum short anteroposteriorly and symmetrically tapered, extending anteriorly from buccal and lingual extremities of base of protolophid. Paracristid arises ventrolingual to protoconid apex, descending anterolingually onto anterior cingulum. Paracristid then bifurcates, with main component curving lingually and thickening into a rounded eminence, while a short ridge continues anterolingually to edge of anterior cingulum. Lingual extreme of paracristid met by a very slight premetacristid descending anteriorly from metaconid apex, then folding buccally across anterior face of protolophid. Two anteroposteriorly orientated enamel crenulations are present on anterior face of M_1 protolophid. Four fine, barely separable crenulations descend from anterior face of M_2 protolophid into trigonid basin. Anterior face of hypolophid with several very fine anteroposteriorly orientated enamel crenulations descending into interlophid valley. Posterior face of hypolophid bears a similar triangular inflation to dP_3, but is more marked, with distinct shelves formed on buccal and lingual sides.

Comparison with other taxa

Due to the juvenile nature of the *S. brachyselenis* holotype, it is not useful to compare the mandibular characters with those in the descriptions of most other sthenurines as they are largely based on adult specimens. The holotype was therefore compared with the only *Sthenurus* species for which similarly aged specimens are known, namely *S. occidentalis* Glauert 1910, *S. brownei* Merrilees 1967, *S. maddocki* Wells and Murray 1979, *S. pales* DeVis 1895, *S. andersoni* Marcus 1962 and *S. gilli* Merrilees 1965. Dental comparisons were also made with adult specimens of *S. cegsai* Pledge 1992 and *S. oreas* DeVis 1895 (see Appendix 1). In both size and shape of the mandible, *S. brachyselenis* is most similar to *S. occidentalis,* but the ramus is relatively deeper for most of its length (Fig. 2). Morphology of the symphysial union, the degree to which I_1 is upturned and relative length of the diastema are also similar to *S. occidentalis.* However, the unworn occlusal surface is quite straight in *S. brachyselenis,* a characteristic only observed previously in the very slender and elongate I_1 of *S. maddocki* (Wells and Murray 1979; Fig. 2).

P_2 is very similar in morphology to P_3, although it is only around half the length and relatively wider. The P_3 of *S. brachyselenis* is most similar (Fig. 3) to the plesiomorphic early Pliocene *S. cegsai,* from Corra Lynn Cave, Yorke Peninsula, South Australia (Pledge 1992), and is shorter relative to M_1 than any other *Sthenurus* species. Both *S. brachyselenis* and *S. cegsai* have a relatively narrow P_3 dominated by the main crest divided into five cuspules. The buccal crest is very short in both species, although the crest appears to have been straighter in *S. cegsai,* and is positioned very close to the posterior extremity of the main crest. This results in a very narrow median valley, unlike *S. brachyselenis,* and also means that the *S. cegsai* P_3 is only slightly wider posteriorly than anteriorly. *S. brachyselenis,* in contrast to the holotype of *S. oreas* (QM F2923) and the only other conspecific for which P_3 is known (AM MF90 — see Tedford 1966, Fig. 14), possesses a very short buccal crest which does not join with the main crest anteriorly, has a main crest that is markedly curved posteriorly and two transverse ridgelets which dominate the median valley. The very limited degree to which these characters vary within species known from large samples (20 to 150 individuals of *Sthenurus occidentalis, S.*

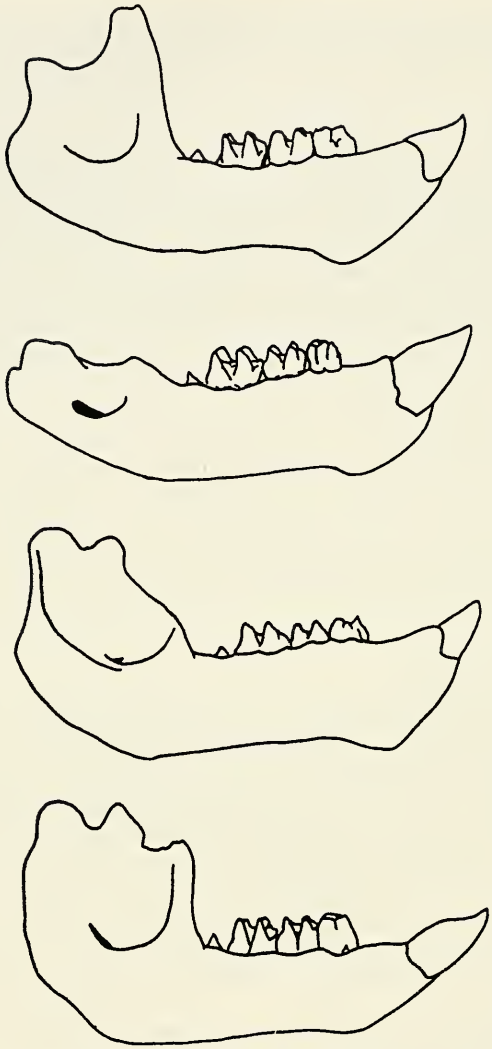

Figure 2. Juvenile mandible outlines of a) *S. occidentalis*, b) *S. brachyselenis*, c) *S. maddocki* and d) *S. brownei*, scaled to a common length.

brownei, S. gilli, S. andersoni, S. maddocki) suggests that the differences between *S. brachyselenis* and *S. oreas* are unlikely to be a result of intraspecific variation (cf. Tedford 1966).

In morphology and size, the molariform teeth of *S. brachyselenis* are most similar to *S. brownei* (Fig. 3). The teeth are similarly low crowned, lophids are linear and close to parallel, the anterior cingulum is relatively narrow (laterally), the cristid obliqua and paracristid are low, but well-formed and aligned on the buccal side of the tooth, and the posterior face of the hypolophid bears a marked triangular-shaped inflation. However, in contrast, the anterior cingulum is shorter and not symmetrically tapered in *S. brownei,* and the lophid faces are more coarsely crenulated. The manner in which the paracristid bifurcates anteriorly also differs between these species. In *S. brownei* and *S. pales* the

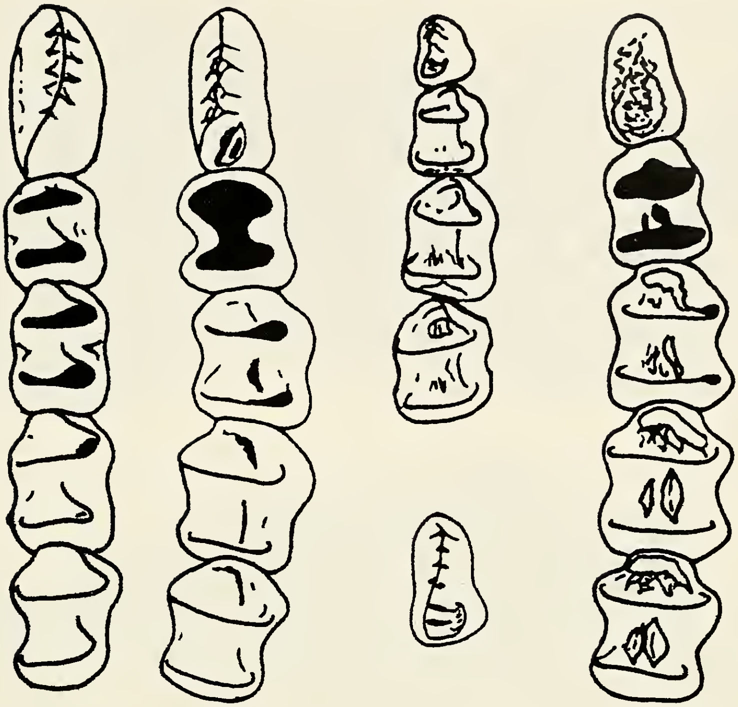

Figure 3. Comparison of cheek teeth of a) *Hadronomas puckridgi* P3, Ml-4; b) *Sthenurus cegsai* P3, Ml-4; c) *S. brachyselenis* P2, dP3, Ml-2, P3; and d) *S. oreas* P3, Ml-4.

transverse component of the paracristid is either thickened anteroposteriorly forming a lozenge shape, or reduced to tiny cuspules. The anteriorly directed fork is only slight and variably present in these two species. In *S. maddocki* and *S. euryskaphus* a bifurcated paracristid is also evident, but the transverse component is larger and more completely formed than the aforementioned species, curving across the anterior cingulum. Among sthenurines, the anteriorly directed fork is expressed to the greatest degree in *Procoptodon,* its function appearing to be as a buttress for the typically high paracristid.

On comparison with *S. oreas,* a triangular-shaped inflation on the posterior face of the hypolophid is incipient in one of the three mandibular specimens referable to that species, AM F88541 (= MF1). The manner in which the *S. brachyselenis* paracristid bifurcates anteriorly is also expressed to a similar, but slightly lesser degree in AM F88541. However, the lower molars of *S. oreas* can be separated in the following ways:

1. The anterior cingulum is not symmetrically tapered and does not extend to the lingual extremity of the base of the protolophid. Additionally, in the holotype, it does not extend to the buccal extremity of the base of the protolophid.
2. The paracristid and cristid obliqua are thicker and higher.
3. A thick accessory crest is positioned lingual and parallel to the cristid obliqua.

Phylogenetic affinities

Using the late Miocene sthenurine *Hadronomas puckridgi* for comparison, all species of *Sthenurus* bear a buccal crest (raised buccal cingulum) adjacent to the main crest on P_3, molars that are wider relative to their length, lophids orientated very close to perpendicular to the longitudinal axis of the tooth, and at least a few very fine enamel crenulations on the molar lophid faces. Within *Sthenurus,* there is a general evolutionary trend toward elongation of the buccal crest on P_3. This is barely more than a posterobuccal cusp in the early Pliocene *S. cegsai,* but runs most of the length of the tooth in derived Pleistocene species, such as *S. pales.* Likewise, the pairing of low crowned molars with a few fine or no enamel crenulations on the lophid faces is characteristic of *S. cegsai* and *Hadronomas,* but all of the Pleistocene species have either low crowned molars with many fine or a varying number of coarse enamel crenulations (eg., *S. occidentalis, S. brownei*), or high crowned molars with very few fine or no enamel crenulations (eg., *S. andersoni, S. stirlingi*). Low crowned, heavily crenulated molars combined with brachycephaly, are adaptations to heavier browsing, while high crowned, weakly crenulated molars combined with dolichocephaly, and hypertrophy of the paracristid and cristid obliqua led Tedford (1966) to suggest a reversion to a largely grazing habit in these species.

Therefore, possession of low crowned molars with few fine enamel crenulations, a low paracristid and cristid obliqua positioned close to the buccal side of the molar, and a narrow P_3 with a very short, buccal crest must suggest that *S. brachyselenis* occupies a relatively plesiomorphic phylogenetic position among *Sthenurus,* and is only derived relative to the early Pliocene *S. cegsai.* It is conceivable that *S. brachyselenis* could be a precursor to *S. oreas,* but presence of a strong paracristid, cristid obliqua and interlophid accessory crest, and long buccal crest on P_3 joining to the main crest anteriorly, suggest that a direct ancestor-descendant relationship is most unlikely.

Sthenurus (Simosthenurus) euryskaphus sp. nov.
(Figs 4–6)

1966 *Sthenurus oreas* Tedford, p. 39–41, fig. 15.
1976 *Sthenurus oreas* Marcus, p. 69–70.

Holotype

AM MF2, left juvenile ramus, with dP_3, M_1, M_2, P_3 excavated from body of mandible. Associated I_1 described and figured by Tedford (1966) appears to be lost. P_2, M_3 not preserved, although alveoli indicate both teeth were fully erupted.

Type locality and age

The holotype was collected in 1887 by W. Anderson from Bone Camp Gully, adjacent to Myall Creek, near Bingara in northeastern New South Wales (29°50'S, 152°30'E). Age of the type locality is middle Pleistocene (Marcus 1976).

Diagnosis

P_3 short relative to width, with median valley very wide and rather circular due to very lingually convex posterior component of main (lingual) crest and buccally convex buccal crest. Lower molars very similar in size and morphology to eastern *Sthenurus occidentalis,* but with slightly narrower anterior cingulum and fewer fine enamel crenulations on lophid faces. Juvenile mandible differs from *S. occidentalis* in bearing large digastric eminence and sulcus, and large, deep symphysis with long posterior extension below genial pit.

Figure 4. *Sthenurus euryskaphus* sp. nov. holotype (AM MF2): a) mandible in lateral view; b) mandible in medial view; c) stereopair of mandible and cheek tooth row in occlusal view; d) stereopair of P_3 in occlusal view. Scale in millimetres.

Etymology

Gr. *eury-* 'broad', *skaphe* 'basin, trough', in reference to the broad nature of the median valley or basin formed between the main (lingual) and buccal crests on P_3.

Description

Juvenile ramus deep for width, particularly in region of symphysis and digastric eminence. Anterior region of symphysial union not preserved, but deep and rugose central and posterior regions indicate strong mandibular ankylosis. Posterior region of symphysis extends well below genial pit forming a prominent boss. Digastric eminence long and deep, with sulcus large and deep, extending anteriorly to below M_2 protolophid. Posterior portion of I_1 alveolus large and orientation of longitudinal axis indicates tooth was very upturned relative to cheek tooth row (see also Tedford 1966, fig. 15). Little of diastema preserved, but appears to have been relatively short. Only deep, anteriormost portion of buccinator sulcus is preserved. Anterior mental foramen circular in cross-section, opening more dorsally than laterally, with dorsal border immediately below anterior extreme of buccinator sulcus. Posterior mental foramen positioned relatively high on mandible, below hypolophid of M_1. Most of posterior region of mandible broken away, preserving only broken anterior root of ascending ramus, small part of anteroventral border of masseteric fossa and large, near vertical masseteric canal. Posteriorly, on mesial side of mandible, a sharp anterodorsally orientated process is present and appears to have partially overhung mylohyoid groove.

Alveolus of P_2 indicates tooth was slightly shorter than dP_3. dP_3 completely molariform, with protolophid markedly tapered buccally toward relatively narrow occlusal surface. Cristid obliqua low, descending anterolingually from hypoconid, then curving more anteriorly to posterior face of protolophid, before trending buccally to terminate at protoconid apex. Very low pre-entocristid directed anterobuccally from entoconid apex met in interlophid valley by low postmetacristid descending posterobuccally from metaconid apex. Posterior extreme of paracristid shifted slightly lingually along anterior face of protolophid from protoconid apex. Anteroposteriorly orientated component of paracristid short, and turning into longer tranverse component which terminates near to lingual extreme of anterior cingulum. Premetacristid directed buccally across anterior face of protolophid, which also bears two central, anteriorly directed, fine enamel crenulations. Anterior face of hypolophid bears no enamel crenulations. Posterior face of hypolophid with low, barely detectable postentocristid which descends ventrobuccally from entoconid apex to about one third of way down tooth crown, then curves up centrally, then trends ventrobuccally once again. This produces a very shallow, rather sinusoidal inflation across the posterior hypolophid face.

P_3 wide relative to length and nearest to, although slightly shorter than M_2 in length. Posterobuccal aspect of tooth slightly inflated and bearing a buccally convex, crescentic crest. Main crest divided into four cuspules linked to one another by short ridgelets. Prominent, anteriormost cuspule bears two thick posteroventrally directed ridgelets descending from apex; one lingual, one buccal. Main crest extends posterolingually, curving even more lingually toward posterior extreme, then descending to terminate posterior to median valley. At this point, posterolingual extreme of buccal crest also terminates, resulting in a V-shaped notch when viewed posteriorly. Median valley is very wide and rather circular, with many fine ridgelets descending into centre of valley. Anterior extreme of buccal crest connected to buccal side of second cuspule of main crest by low transverse ridgelet.

M_{1-2} low crowned with protolophid and hypolophid occlusal surfaces linear and close to parallel. Anterior turn on lophid ends emphasised buccally. Cristid obliqua and paracristid low, but well-formed, and shifted slightly lingually along anterior lophid faces from buccal extreme of tooth. Anterior cingulum not extended across entire base of protolophid and only tapered anteriorly on buccal side. Paracristid trends anteriorly from position on protolophid anterior face slightly ventrolingual from protoconid apex, before turning lingually. Anteroposteriorly orientated component of paracristid slightly shorter than transverse component, which terminates at lingual extreme of anterior cingulum. Several fine enamel crenulations descend into trigonid basin from anterior protolophid face. Similarly, several anteroposteriorly orientated enamel crenulations arise from anterior hypolophid face, but these are very fine and terminate before reaching interlophid valley. Posterior face of hypolophid is characterised by a triangular-shaped inflation, much more pronounced than in dP_3. A very shallow and barely detectable postentocristid descends to a position in ventrolingual region of posterior hypolophid face. From here, shelf-like crest turns and trends dorsobuccally to a point, before trending to ventrobuccal corner of posterior hypolophid face. In this region, shelf becomes less distinct and more of an inflation.

Comparison with other taxa

As with *S. brachyselenis,* it is most useful to compare the juvenile holotype of *S. euryskaphus* with similarly aged specimens in order to elucidate any unique features of the mandible. The holotype was compared with juvenile specimens of *S. occidentalis, S. brownei, S. pales, S. gilli,* and a widespread species referred to herein as *Sthenurus* 'P17250' (see Appendix 1). The latter species is currently under description elsewhere. A comparison was also made with adult representatives of *S. antiquus* and *S. oreas,* and Tedford's (1966) sketch of AM MF90, which is a juvenile *S. oreas* mandible slightly older ontogenetically than the *S. euryskaphus* holotype.

In size and general shape, the juvenile mandible is most similar to *S. occidentalis* and *S.* 'P17250' (Fig. 5). *S. euryskaphus* differs from *S. occidentalis* in its greater ramus depth relative to width, longer and deeper extension of the posterior region of the symphysis below the genial pit, more pronounced digastric eminence, and possession of a sharp process overhanging the mylohyoid groove. *S. euryskaphus* differs from *S.* 'P17250' in being slightly more robust, possessing a relatively shorter ramus, a longer and deeper extension of the posterior region of the symphysis below the genial pit, and more upturned I_1. On comparison with Tedford's sketch of MF90, it appears that the anterior border of the mandible is more steeply inclined and straighter in *S. oreas,* the digastric eminence is less prominent and the ventral border of the masseteric fossa is higher. Although only one adult ramus is known for *S. antiquus,* considering the differences in their ontogenetic age, the general dimensions (size, shape, development of the digastric sulcus) are not unlike what might be predicted for an adult *S. euryskaphus.*

In morphology, absolute size, and size relative to the succeeding molars, the P_3 of *S. euryskaphus* is similar to *S.* 'P17250', but also bears some resemblance to *S. oreas.* Like *S.* 'P17250', the P_3 is short relative to M_1 and bears a relatively short buccal crest. *S. euryskaphus* can be distinguished from *S.* 'P17250' by its large lingual convexity of the main crest posteriorly, the slightly longer buccal crest, and much wider, open median valley. In size, *S. euryskaphus* differs from the holotype of *S. oreas* in its greater size, but cannot be separated from the species on this basis because it is very similar to AM MF90 in premolar dimensions (measurements from Tedford 1966). Morphologically though, the P_3 of *S. euryskaphus* is slightly wider relative to its length, has a shorter, more crescentic buccal crest without a strong connection with the main crest anteriorly, and a more circular and slightly wider median valley (Fig. 6). The *S. euryskaphus* P_3 is easily distinguishable from *S. antiquus,* being much smaller in size, shorter relative to molars, wider relative to length, and bearing a shorter, wider median valley and a shorter, more curved buccal crest. *S. euryskaphus* is easily separable from *S. occidentalis, S. brownei, S. gilli* and *S. pales,* as the P_3 of these species is longer relative to molar size, they have a narrower median valley bordered by a much straighter main crest, and a longer buccal crest

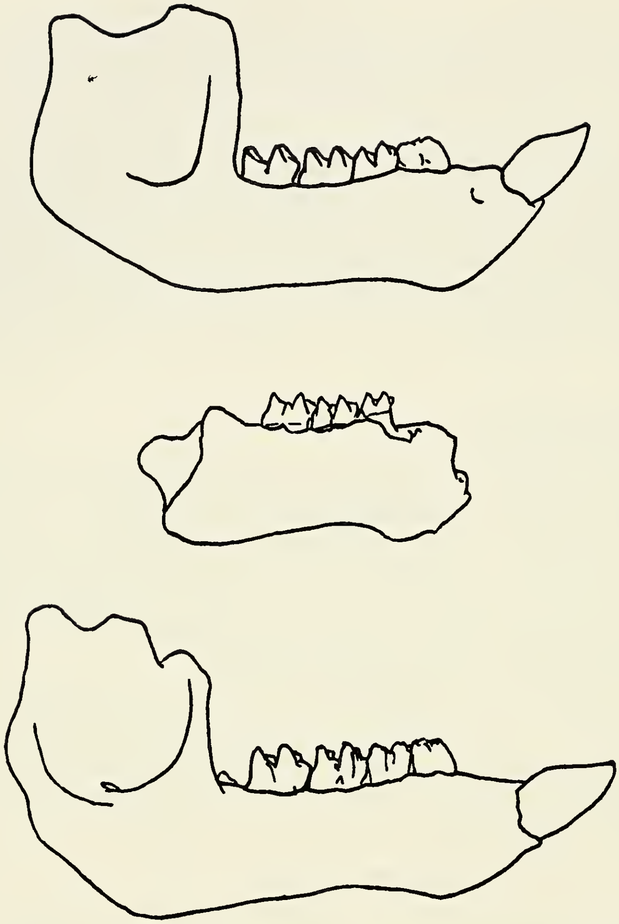

Figure 5. Juvenile mandible outlines of a) *S. occidentalis*, b) *S. euryskaphus* and c) S. 'P17250', scaled to a common depth below the M_2 protolophid.

which joins with the main crest anteriorly.

The molariform teeth of *S. euryskaphus* are most similar to *S. occidentalis* and *S. antiquus* in almost all characters observable (Fig. 6). The cristid obliqua and paracristid are similarly positioned and orientated, but not quite as shifted lingually. The anterior cingulum and transverse component of the paracristid are most similar to *S. occidentalis,* but the cingulum is slightly narrower overall. In *S. antiquus,* the cingulum is wider, and shorter anteroposteriorly. The morphology of the posterior hypolophid face in *S. euryskaphus* is characterised by a triangular-shaped inflation, with a short shelf formed along its dorsal border. This is similar to *S. occidentalis,* but a dorsal shelf is only barely detectable. In this feature, it is intermediate between *S. occidentalis* and *S. brownei.*

A few fine vertical enamel crenulations are present lingual to the paracristid in *S. euryskaphus,* which is intermediate in morphology between the many fine crenulations on the anterior protolophid face of *S. occidentalis* and the very few fine crenulations present in *S. antiquus.* Similarly, there are a few fine enamel crenulations lingual to the cristid obliqua on the anterior hypolophid face of *S. occidentalis,* few very fine crenula-

Figure 6. Comparison of cheek teeth of a) *S. euryskaphus* dP_3, M_{1-2}, P_3; b) *S. antiquus* P_3, M_{1-4}; c) *S. occidentalis* P_3, M_{1-4}; d) S. oreas P_3, M_{1-4}.

tions on the *S. euryskaphus* hypolophid, and only the barest remnant of very fine crenulations in *S. antiquus.* Previously, Marcus (1976) referred to the similarity between the enamel crenulations of MF2 and *S. occidentalis,* although observed that the molars of the latter were smaller. However, the comparison was made with the typically small topotypic material from Western Australia, not specimens from eastern Australia with which *S. euryskaphus* compares favourably in size. Work in progress indicates that *S. occidentalis* may be synonymous with *S. orientalis* Tedford 1966, each representing the morphological extremes of a geographic cline. Overall, in general molar outline and width relative to length, *S. euryskaphus* is similar to both *S. antiquus* and *S. occidentalis.*

S. euryskaphus is separable from *S. oreas* in that the posteriormost component of the paracristid is orientated almost directly anteroposteriorly, not anterolingually; the transverse component of the paracristid is larger; the enamel crenulations on the anterior lophid faces are much finer and there is no thick accessory crest positioned lingual to the cristid obliqua.

Phylogenetic affinities

While doubt is an inherent part of the description of new morphological species from very limited material, especially where well-represented related taxa display a significant amount of intraspecific variation, an appreciation of the most variable characters minimises the chances of future synonymy. *S. euryskaphus* bears a resemblance to the variable *S. occidentalis,* but the characters by which it is distinguishable are not highly variable within *S. occidentalis.* Most variation in mandibular and dental characters is size-based, either absolute or proportional. Tedford (1966) attributed MF2 to *S. oreas* because he considered it within the probable morphological range of that species. However, disparity in the morphology of the mandible, P_3 and molars, strongly suggest that MF2 does not belong within *S. oreas,* or within any other previously named taxon.

The overriding number of similarities shared with *S. occidentalis, S.* 'P17250' and *S. antiquus* is likely to imply a relatively close phylogenetic relationship with these species. Low crowned, low complexity molars and a short, wide anterior cingulum appear to be plesiomorphic characters within the genus, as exemplified by *S. cegsai* and *S. brachyselenis.* Although the molars are larger and higher crowned, these features are similar in *S. antiquus,* known from the late Pliocene of southeastern Queensland (Bartholomai 1963). As molars tend to be more conservative evolutionarily, this may indicate that *S. euryskaphus* is more derived than *S. antiquus.* Although the P_3 of *S. antiquus* is considerably larger, and the buccal crest longer and straighter, if this crest were simply curved buccally, then posterior premolar width would be increased and the median valley widened, producing a very similar form to *S. euryskaphus.* It appears very likely that *S. occidentalis* is more derived, given its more complex molar morphology, and presence of a long buccal crest connected to the main crest anteriorly on P_3. Although the phylogenetic position of *S.* 'P17250' is uncertain and currently under consideration elsewhere, it is likely to be less derived than *S. euryskaphus,* given the very short buccal crest on P_3, close proximity of the cristid obliqua and paracristid to the hypoconid and protoconid, paucity of molar enamel crenulations, and absence of a shelf on the posterior hypolophid face.

Bartholomai (1963, 1972) and Tedford (1966) have suggested a close phylogenetic association, perhaps even ancestor-descendant relationship between the late Pliocene *S. antiquus* and Pleistocene *S. oreas.* The latter is certainly more derived, but a close alliance is unlikely given the disparity in molar complexity, premolar morphology and premolar length relative to the molars. *S. oreas* is clearly a very derived member of the genus and it is not surprising that De Vis (1895) synonymised *Procoptodon* with *Sthenurus* based on these dental characters. Tedford (1966) considered the dental similarities between *S. oreas* and, in particular, *Procoptodon pusio* a likely result of parallel evolutionary trends, but *S. oreas* also resembles *Procoptodon* in the robustness of its ramus and massive opening for the insertion of the deep masseter. These craniodental similarities and the absence of pre-Pleistocene *Procoptodon* remains seem more likely to indicate that the genus has arisen from within *Sthenurus,* possibly in the vicinity of *S. oreas.*

CONCLUSIONS

Sthenurus brachyselenis bears closest affinity with the early Pliocene *S. cegsai* from Corra Lynn Cave, Yorke Peninsula, South Australia, possessing low crowned, simple molars and a narrow P_3 bearing a very short, buccal crest. It is more derived than *S. cegsai,* but plesiomorphic relative to all other *Sthenurus* species. As such, it displays a stage of evolution hitherto unrepresented by any described taxon.

Characters shared or intermediate in expression between *S. occidentalis, S.* 'P17250' and *S. antiquus* imply that *S. euryskaphus* is phylogenetically close to these taxa. *S. antiquus* appears to be more plesiomorphic, possessing low complexity molars with short, wide anterior cingula, characters shared with the plesiomorphs *S. cegsai* and *S. brachyselenis.* In contrast, *S. occidentalis* is considered more derived than *S. euryskaphus,* due to its greater molar complexity and long buccal crest connected to the main crest anteriorly on P_3.

The removal of both AM F31026 and MF2 from *S. oreas* has impelled a reconsideration of the phylogenetic position of that species. *S. oreas* appears to represent a very derived species of *Sthenurus,* sharing several important dental and mandibular similarities with *Procoptodon,* in particular *P. pusio.* This may point to a paraphyletic origin for *Procoptodon* from within *Sthenurus,* a view supported by the absence of *Procoptodon* remains from pre-Pleistocene deposits.

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APPENDIX I

Material used for comparison with *S. brachyselenis* and *S. euryskaphus*. AM = Australian Museum, FU = Flinders University, QM = Queensland Museum, SAM = South Australian Museum.

Species	Registration Number	Locality
Sthenurus andersoni	SAM P20636, FU0463	Victoria Fossil Cave, Naracoorte SA
S. brownei	SAM P20713, P25604, P27796, P27798, FU0273	Victoria Fossil Cave, Naracoorte SA
S. cegsai	SAM P31800 (holotype)	Corra Lynn Cave, Curramulka SA
S. gilli	FU0008, FU0102	Victoria Fossil Cave, Naracoorte SA
S. maddocki	SAM P16518, P16674, P27357	Victoria Fossil Cave, Naracoorte SA
S. occidentalis	SAM P16534, P16536, P16624, P16664	Victoria Fossil Cave, Naracoorte SA
S. oreas	QM F2923 (holotype) QM F3814, AM F88541 (= MF1)	Darling Downs QLD Cement Mills, Gore QLD Wellington Caves NSW
S. pales	SAM P27797	Victoria Fossil Cave, Naracoorte SA
Sthenurus 'P17250'	SAM P17250 SAM P28671, P28996	Greenwater Hole Cave, Tantanoola SA Victoria Fossil Cave, Naracoorte SA